Productivity factors of the Finnish semi-domesticated reindeer *(Rangifer t. tarandus)* stock during the 1990s

Jouko Kumpula[1], Alfred Colpaert[2] & Mauri Nieminen[1]

[1] Finnish Game and Fisheries Research Institute, Reindeer Research Station, FIN-99910 Kaamanen, Finland (jouko.kumpula@rktl.fi).
[2] University of Oulu, Department of Geography, FIN-99870 Oulu, Finland.

Abstract: Intensive reindeer grazing and the increase of other land use forms have caused a decline in the amount of arboreal (*Alectoria, Bryoria* spp.) and reindeer (*Cladina* spp.) lichens in the Finnish reindeer management area during the last few decades. Supplementary feeding of reindeer has increasingly compensated for the lack of natural winter fodder. The amount of the supplementary feeding and the quantity and quality of summer pastures should therefore have an increasing effect on the productivity of reindeer stock. In order to outline better the present carrying capacity problems on pastures in the Finnish reindeer management area we focused some of the most important productivity factors of Finnish reindeer stock from 1993 to 1999. The results showed that the productivity of reindeer stock in Finland was dependent especially on two main elements: amount of reindeer feeding and reindeer densities on summer pastures. Winter pastures had no clear effect on productivity when analysing the entire management area. High productivity figures in reindeer stock (calf production, carcass mass and meat production per reindeer) were reached in the management districts where winter feeding was the most abundant, reindeer densities relatively low and summer pastures abundant. An increase in reindeer density on summer pastures raised meat production per total summer pasture area but decreased carcass mass of reindeer calves and meat production per reindeer. It seems that the fundamental factor for keeping the reindeer stock productivity sustainable at a high enough level is to optimize the long-term reindeer densities on pastures. Summer pastures may gradually become a limiting factor for reindeer stock productivity in some areas if overgrazed and decreased winter pastures are only compensated for by winter feeding of reindeer.

Key words: carrying capacity, feeding, reindeer, stock productivity, summer pastures.

Rangifer, 22 (1): 3-12

Introduction

Wide fluctuations in stock numbers are very typical for several reindeer and caribou populations (*Rangifer tarandus*) belonging to the genus *Rangifer* (Klein, 1968; Henry & Gunn, 1991; Messier *et al.,* 1988; Post & Klein, 1999). Even though the ultimate reason for collapses in reindeer or caribou populations can be found in harsh snow and weather conditions in winter, the collapses are almost always preceded by the gradual deterioration of animal nourishment in pastures. The increasing herbivore population causes a slowly progressing, but continuous change in the composition, biomass and productivity of plant species on the most important pasture areas, especially in those plants which are most important as fodder for herbivores (Klein, 1968; Leader-Williams *et al.,* 1987; Henry

& Gunn, 1991; Manseau *et al.,* 1996; Augustine *et al.,* 1998; Crête & Doucet, 1998; Alpe *et al.,* 1999). These vegetation changes may take place so gradually that their documentation over a period of years can prove very difficult (Wegener & Odasz-Albrigtsen, 1998). Besides this, variation in climatic conditions during the growing season and its effects on vegetation can sometimes temporarily obscure the change in vegetation caused by herbivore grazing (McCullough, 1992; Fynn & O'Connor, 2000).

Natural grazing systems of herbivores have been suggested to be divided into two types: equilibrium and non-equilibrium systems (Ellis *et al.,* 1991; Behnke & Scoones, 1992; Fox, 1998). In equilibrium systems, there should be predictable interactions between the herbivore population and its food resources. On the contrary, in non-equilibrium systems these kinds of predictable interactions should be weak and irregular. It has also been argued that the concept of carrying capacity could not be useful in stochastic environments for describing plant-herbivore dynamics (e.g. McLeod, 1997). Some proposals have also been made to apply the non-equilibrium theory to pastureland management of reindeer management (Fox, 1998; Tyler, 1998; Colman, 1999). However, there are several studies which show the existence of the long-term predictable interactions between reindeer populations and their food resources despite the fact that all real natural grazing systems always involve unpredictable and irregular elements.

McLeod (1997) concluded that the interactive carrying capacity model (Caughley, 1976; 1979; Caughley & Lawton, 1981) was suitable for calculating carrying capacity in both deterministic and stochastic environments. According to this model there are several equilibria between herbivore population and its food resource but only the economic carrying capacity equilibrium gives the highest sustained yield in animal production. In some other models (McCullough, 1979; Dasmann, 1981), the maximum sustained yield (MSY) or the carrying capacity equilibrium corresponding to it represents the economic carrying capacity equilibrium of the interactive model. However, understanding the equilibrium between herbivore population and its food resources as a fixed or steady point in real natural grazing systems can lead to a misunderstanding of the whole operation of population regulating and limiting factors. What the real causes of oscillations in a certain natural herbivore population are, and what the potential carrying capacity of the range occupied by this population is, are two very different although interlinked questions.

Increase in the number of reindeer during the last few decades and the resulting rising pressure on pastures in the Finnish semi-domesticated reindeer management area (Fig. 1), have caused deterioriation in conditions of lichen ranges (Mattila, 1988; 1996). Other forms of land use have also probably affected the condition of lichen pasture, but have especially decreased the amount of old forest which previously formed the important late winter pasture resource (Kumpula & Nieminen, 1992). As a consequence, the amount of reindeer lichens (*Cladina* spp.) and arboreal lichens (*Alectoria*, *Bryoria* spp.) on reindeer pastures has decreased markedly in Finland. According to their model Kumpula *et al.* (2000) estimated that the average lichen biomass in lichen ranges in the whole management area in the middle of 1990s was only 13% of the optimum and 5% of the climax stage lichen biomass. This development in winter ranges and natural winter fodder in Finland

Fig. 1. The semi-domesticated reindeer management area in Finland formed by the 56 separate reindeer management districts.

has intensified supplementary feeding of reindeer in winter (Nieminen & Autto, 1989; MMM, 1999).

Both lichen ranges and arboreal lichen pastures affected the productivity of reindeer stock before the mid-1990s in the northern part of the Finnish reindeer management area (Kumpula & Nieminen, 1992; Helle & Kojola, 1994; Kojola *et al.,* 1995; Kumpula *et al.,* 1998). The amount and condition of winter ranges affected both calf production and carcass mass of reindeer. Reindeer densities on total range land had the strongest effect on carcass mass. The amount of supplementary feeding in winter was not yet clearly correlated to productivity but intensive calf slaughtering clearly raised productivity. Towards the end of the 1990s supplementary feeding has also increased in the northern part of the management area and condition of lichen ranges in some of the studied districts has deteriorated (Kumpula *et al.,* unpubl.) although there was some reduction in the number of reindeer in this area in the late 1990s. Since supplementary feeding more and more compensates for the lack of natural winter fodder in Finland, we suppose that there is no longer a clear correlation between winter pastures and reindeer stock productivity. On the contrary, the amount of supplementary feeding and quantity and quality of summer pastures should affect the productivity.

In order to outline better the present carrying capacity problems on pastures in the Finnish reindeer management area we focused some of the most important productivity factors of Finnish reindeer stock from 1993 to 1999. Especially effects of reindeer densities on lichen, arboreal lichen and summer pastures, the amount of summer fodder and supplementary feeding per reindeer on stock productivity were analysed.

Material and methods

Inventories of reindeer pasture resources in all 56 reindeer herding-districts in the Finnish reindeer management area were collated for winter pastures in the period 1995-96 and for summer pastures in 1997-98 (Kumpula *et al.,* 1997; 1999). The main pasture types, both winter and summer pastures, were classified and mapped using Landsat-5 TM images using noteworthy field site data (see Colpaert *et al*., 1995; Colpaert, 1998). Accuracy of the classified satellite images was on average 80%. The area (km^2) of the main pasture types in each reindeer management district was calculated according to the classifications. All dry and very dry vegetation types were included in lichen pastures while all old and mature (over 80 years old) pine forests were included in arboreal lichen pastures. All mires and all submesic and mesic vegetation types were included in summer pastures.

In summer pasture inventory, the average biomasses of all hay-, sedge- and grass like plants, dwarf shrubs (*Vaccinium myrtillus* and *V. uliginosum*) and deciduous leaf fodder in each summer pasture type was calculated for all vegetation zones on the basis of the field site data (1494 sites). Firstly, coverage of the plant groups was estimated in ten vegetation plots (bottom area 1.0 m x 1.0 m and height 1.5 m) in each site on field. All plants in these five plants groups were collected and dried (dry weight) systematically in two of ten plots. Data from the coverage and biomass measurements were then used to estimate the biomass values for all main vegetation types in each vegetation zone. The gross amount of summer fodder in each reindeer management district was then calculated on the basis of the area of various summer pasture types and the average summer fodder biomass in each pasture type.

The average number of reindeer (winter stock) in each reindeer management district in the period 1993-99 was calculated on the basis of the statistics kept by the Association of Finnish Reindeer Herding Cooperatives (Poromies, 1994-2000). The average reindeer density on lichen, arboreal lichen and summer pastures for each district was then calculated. For lichen and arboreal pastures this density can be kept as a number of all reindeer (adult + calves) grazed per km^2 lichen or arboreal lichen pasture in winter and for summer pasture this density can be kept as a number of reindeer over one year old grazed per km^2 summer pasture in summer. The total biomass of summer fodder per reindeer over one year old (kg/reindeer) was also calculated. Additionally, the average calf production (%), carcass mass of calves (kg) and meat production per reindeer (kg/reindeer) and per summer pasture area (kg/km^2) from 1993 to 1999 in each district was calculated from statistics. Calf production is recorded as the number of calves counted per 100 females over 1.5 years old during the slaughtering period (October-January). Carcass mass of calves was calculated on the basis of the annually reported mean carcass mass of all slaughtered reindeer and the number of slaughtered calves and adults in each year in each district assuming the proportion of calf to adult carcass mass to be 0.63:1.00. Meat production per reindeer (kg/reindeer, winter stock) and per summer pasture area (kg/km^2) was calculated on the basis of the number of all slaughtered reindeer and the mean carcass mass of reindeer.

The Association of Reindeer Herding Cooperatives surveyed the amount of reindeer feeding in the management area twice during the 1990s, in the herding years 1993-95 and 1998-99. On the basis of these two data sets we calculated the average amount of feed used per reindeer (calves + adults) during winter in each district. However, these statistics contain some weaknesses, since the total amount of feed reported from each reindeer management districts have been reported only as kilograms. The nutritional value of feed used can be assumed to approximate that of dry hay (8.8 MJ/kg).

Based upon inventories of reindeer pastures and population parameters we analysed the effect of reindeer densities (on lichen, arboreal lichen and summer pastures) and reindeer feeding on calf production, carcass mass of calves and meat production per reindeer in the period 1993-99 in step-wise regression models. After that we applied regression equations with different degrees of polynomials (curves) to the data for studying the effect of the most important independent variables on dependent variable in more detail. In these models we also substituted reindeer density on summer pastures for the amount of summer fodder available per adult reindeer in order to test the potential improvement of the models. Finally we studied the dependence of meat production per summer pasture area (kg/km^2) both on reindeer density on summer pasture area and feeding at the same time in the multiple regression models. After linear model we fitted different degrees of polynomials in the model in order to see if the relationship between reindeer density on summer pasture area and meat production per summer pasture area is convex shaped. This could be one sign that the economic carrying capacity of summer pastures has been exceeded.

Results

Reindeer density on the most important winter pastures had no clear effect on stock productivity in the period 1993-99 in the entire Finnish reindeer management area. In the step-wise regression models, variation in calf production between the reindeer herding districts in the period 1993-99 seemed to be significantly positively dependent only on the amount of supplementary feed used per reindeer. On the contrary, carcass mass of calves was significantly dependent both on the amount of feed used per reindeer and the reindeer density on summer pastures. Carcass mass of calves increased as feeding of reindeer increased while increasing reindeer density on summer pastures decreased carcass mass. Meat production per reindeer was related to the amount of feed used per reindeer and reindeer density on summer pastures. In the same way as in carcass mass, meat production per reindeer increased as feeding of reindeer increased while increasing reindeer density on summer pastures decreased meat production per reindeer (Table 1).

Making more detailed analyses of the effect of each independent variable on stock productivity can confuse the fact that there was a correlation between the amounts of supplementary feed and reindeer density on summer pastures (r=-0.576, n=56, P<0.001). However, tolerance values in the table 1 indicated that collinearity was not a problem in our data. Also, when we analysed collinearity between the independent variables by condition indices in the previous step-wise regression models we found that the highest condition index had the value 7.5 (see the method in Wilkinson *et al.*, 1996, p. 254-260). This referred more clearly that collinearity was not a problem since only condition indices over 15.0 suggest potential problem of collinearity and condition indices of over 30.0 indicate a serious problem (Besley *et al.,* 1980).

In the non-linear simple regression model, 38% of the variation in calf production between all the herding-districts was explained by the amount of supplementary feed used per reindeer (Fig. 2). Using multivariate regression equations with diffrent degrees of polynomials for studying the dependence of carcass mass of calves on two independent factors in more detail did not improve the regression coefficient (R^2=0.723, Table 1) markedly and the original linear model was the most proper one (Fig. 3). When we substituted reindeer density on summer pastures for the amount of summer fodder available per reindeer over one year old in this model the regression coefficient was not improved (R^2=0.694, y = 0.00008x + 0.014z + 18.055 where y = carcass mass (kg) of calves; x = available summer fodder, kg/reindeer; z = feed, kg/reindeer; n=56, P<0.001).

The linear model for the dependence of meat production per reindeer on two independent factors (R^2=0.368, Table 1) was not also markedly improved by using polynomial equations in the model and the original linear model was the most proper (Fig. 4). When we substituted reindeer density on summer pastures for the amount of summer fodder available per reindeer over one year old in this model the regression coefficient was little improved (R^2=0.374, y = 0.00012x + 0.020z + 9.561 where y = meat production, kg/reindeer; x = available summer fodder, kg/reindeer; z = feed, kg/reindeer; n=56, P<0.001).

The linear regression model also best depicted

Table 1. Dependence of calf production (%), carcass mass (kg) of reindeer calves and meat production per reindeer (kg/reindeer) on the four variables: reindeer density on lichen pastures (LP), reindeer density on arboreal lichen pasture (AP), reindeer density on summer pastures (SP) and amount of feed (kg) used per reindeer in winter. Backwards step-wise regression model (with Alpha-to-Enter = 0.150) and analysis of variance for full regression.

Dependent	Effect	Coef.	SE	Std Coef	Tolerance	*F*	*P*
	In:						
Calf	Feeding	0.071	0.013	0.598	1.000	30.110	0.000
production	Out:	Part. Corr.					
	Reindeer on LP	-0.029	-	-	0.897	0.045	0.833
	Reindeer on AP	0.088	-	-	0.943	0.410	0.525
	Reindeer on SP	-0.004	-	-	0.669	0.001	0.976
						t	
	Constant	53.103	1.954	0.000		27.176	0.000
	Feeding	0.071	0.013	0.598	1.000	5.487	0.000
			R^2=0.358, *n*=56, *F*=30.109, *P*=0.000				
	In:						
Carcass mass	Reindeer on SP	-0.595	0.141	-0.374	0.669	17.860	0.000
	Feeding	0.013	0.002	0.578	0.669	42.790	0.000
	Out:	Part. Corr.					
	Reindeer on LP	-0.146	-	-	0.824	1.128	0.293
	Reindeer on AP	-0.077	-	-	0.791	0.307	0.582
						t	
	Constant	20.715	0.517	0.000	-	40.036	0.000
	Reindeer on SP	-0.595	0.141	-0.374	0.669	-4.226	0.000
	Feeding	0.013	0.002	0.578	0.669	6.541	0.000
			R^2=0.723, *n*=56, *F*=69.142, *P*=0.000				
	In:						
Meat	Reindeer on SP	-0.696	0.422	-0.220	0.669	2.723	0.105
per reindeer	Feeding	0.019	0.006	0.452	0.669	11.450	0.001
	Out:	Part. Corr.					
	Reind on LP	0.067	-	-	0.824	0.233	0.631
	Reindeer on AP	0.056	-	-	0.791	0.163	0.688
						t	
	Constant	12.956	1.551	0.000		6.174	0.000
	Reindeer on SP	-0.696	0.422	-0.220	0.669	-1.433	0.105
	Feeding	0.019	0.006	0.452	0.669	3.278	0.001
			R^2=0.368, *n*=56, *F*=15.401, *P*=0.000				

the dependence of meat production per km^2 summer pasture area on reindeer density on summer pasture area and amount of feeding (Fig. 5). The linear dependence between reindeer density on summer pasture area and meat production per km? summer pasture area indicated that the economic carrying capacity of summer pastures might not have exceeded altough reindeer densities on summer pastures affected carcass mass of calves and meat production per reindeer.

Discussion

Our results showed that the productivity of reindeer stock in the Finnish reindeer management area in the period 1993-99 was dependent on two main factors: the amount of reindeer feeding and rein-

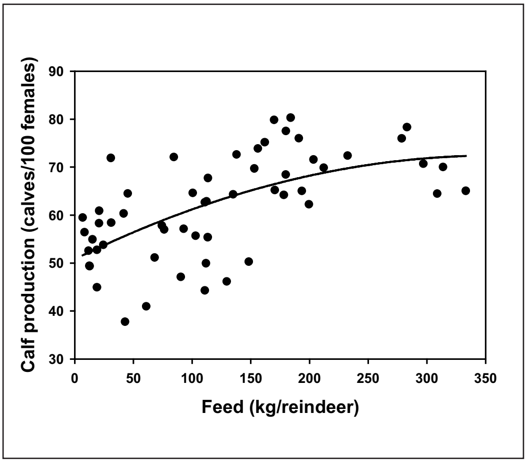

Fig. 2. Dependence of the average calf production in the period 1993-99 on the amount of feed used per reindeer in the Finnish reindeer management area (R^2=0.377, y = 0.121x - 0.0002x^2 + 50.80, n=56, P<0.001).

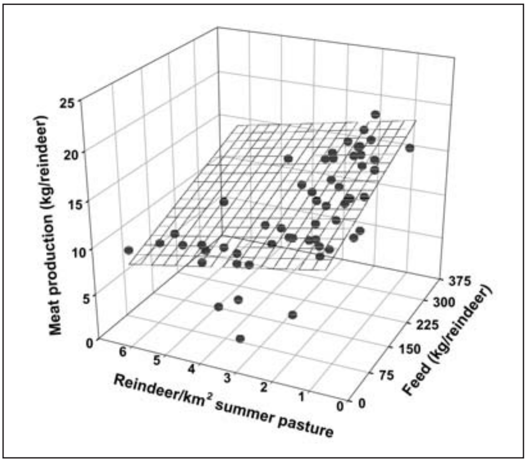

Fig. 4. Dependence of the average meat production per reindeer in the period 1993-99 on reindeer density on summer pastures and feeding of reindeer in the Finnish reindeer management area (R^2=0.368, y = -0.696x + 0.019z + 12.956, where y = meat production, kg/reindeer; x = reindeer/km^2 summer pasture; z = feed, kg/reindeer n=56, P<0.001).

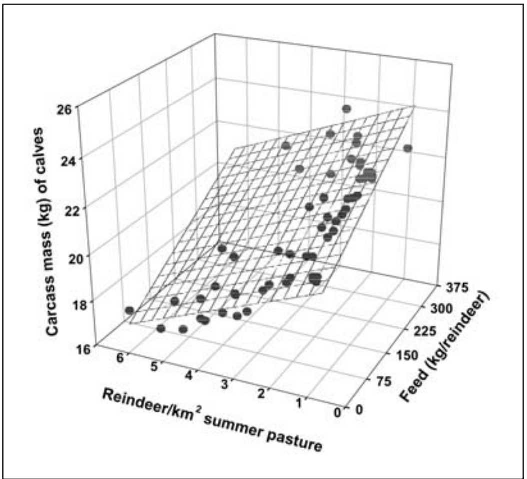

Fig. 3. Dependence of the average carcass mass of reindeer calves in the period 1993-99 on reindeer density on summer pastures and feeding of reindeer in the Finnish reindeer management area (R^2=0.723, y = -0.595x + 0.013z + 20.715 where y = carcass mass (kg) of calves; x = reindeer/km^2 summer pasture; z = feed, kg/reindeer, n=56, P<0.001).

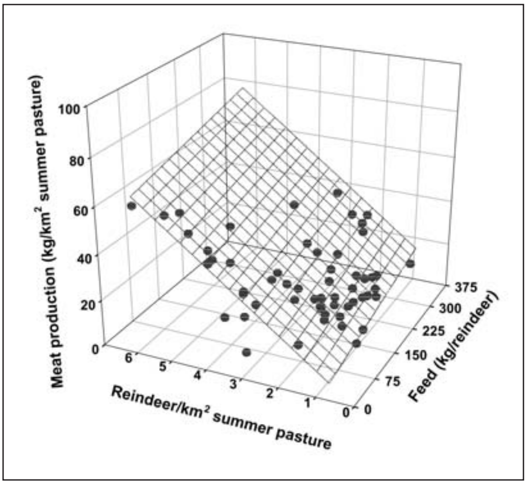

Fig. 5. Dependence of the average meat production per km^2 summer pasture in the period 1993-99 on reindeer on reindeer density on summer pastures and feeding of reindeer in the Finnish reindeer management area (R^2=0.743, y = 11.332x + 0.045z - 2.198 where y = meat production, kg/km^2 summer pasture; x = reindeer density, reindeer/km^2 summer pasture; z = feed, kg/reindeer; n=56, P<0.001).

deer densities on summer pastures. Reindeer densities on the most important winter pastures had no clear effect on stock productivity in this same period when analyzing the entire management area. A decrease in available winter pastures and amount of natural winter fodder has accelerated since the beginning of the 1980s (Mattila, 1988; 1996). This trend has, however, been observed during the whole 1900s (Helle, 1980). Still, in the mid 1990s, around 60% of the variation in the condition of lichen ranges between the reindeer management districts was possible to explain by the average reindeer densities grazed on lichen ranges in 1974-95 (Kumpula *et al.,* 2000). The effects of other land use on the condition of lichen ranges or the amount of old forests have not been studied in the same detail.

While supplementary feeding of reindeer in Finland has increasingly compensated for overgrazed and decreased winter pasture resources, it seems also that the recovery of lichen ranges would be a very long-term and difficult process. Kumpula *et al.* (2000) estimated in their model that the potential recovery time of lichen ranges to the optimal production level without any grazing in Finland in the middle of 1990s was about 18 years. In addition, lichen ranges cover only 3-8% of the total land area in many southern and middle reindeer management districts (Kumpula *et al.,* 1999). This means that even lichen ranges in optimal condition can produce sustainable winter fodder only for a relatively small reindeer herd in these districts. On the contrary, in the northern part of the management area, lichen ranges cover mainly about 20-35% of the land and should therefore form one of the most important criterias for measuring and evaluating the carrying capacity of reindeer ranges.

Supplementary feeding of reindeer has clearly raised the productivity of reindeer stock in Finland (see also Helle & Kojola, 1994). This increase in productivity has also been made possible by the fact that in those districts where feeding was most intensive (southern and middle part of the management area) total reindeer densities were usually relatively low and summer pastures abundant. Therefore the productivity of reindeer stock was not limited by winter or summer pastures but was mainly dependent on the amount of feeding. However, it has to be emphasized that the benefit gained by reindeer feeding in reindeer management, cannot be evaluated only on the basis of the gross productivity of reindeer stock. The costs and other long-term effects of feeding on reindeer management and reindeer stock should also be taken into account.

The long-term effect of heavy summer grazing has been identified as an impotant factor that affects the plant composition and productivity in vegetation communities (Leader-Williams *et al.,* 1987; Henry & Gunn, 1991; Lehtonen & Heikkinen, 1995; Augustine *et al.,* 1998). Overgrazing of summer pastures therefore affects the quantity and quality of summer fodder available for reindeer or caribou (see Ouellet *et al.* 1994; Manseau *et al.,* 1996; Crête & Doucet, 1998). Poor summer food availability causes reduction of body weight of reindeer and may then also reduce calf production. Reindeer are unable to rebuild their body condition and collect enough fat reserves during the summer season if summer ranges are insufficient. The same kind of examples can be found in several *Cervidae* populations, such as reindeer, and caribou (Klein, 1968; Leader-Williams & Ricketts, 1982; Reimers, 1983; Skogland, 1983; 1985; Post & Klein, 1999), red deer (Coulson *et al.,* 1997), roe deer (Hewison *et al.,* 1996) and moose (Sand *et al.,* 1996; Hjeljord & Histøl, 1999). Heavily overgrazed plant communities may also need a very long time to recover to the optimal stage (Klein, 1987; Crête & Doucet, 1998; Kumpula *et al.,* 2000).

It is likely that in the same way as in winter pastures, productivity of summer fodder in the most important summer range areas can be manipulated by adjusting the long-term grazing pressure (see for example Tolvanen *et al.,* 1992; 1993; 1994; Ouellet *et al.,* 1994; Manseau *et al.,* 1996; Crête & Doucet, 1998; Alpe *et al.,* 1999). Varying weather and snow conditions, to which reindeer management always has to adapt, form one essential element in the productivity and availability of fodder plants. However, it has been demonstrated that the effect of these stochastic weather elements had a much smaller effect on the food plant resources than the large fluctuations of herbivore populations (Messier, 1995). Thus the existence of stochastic elements in the reindeer management system does not exclude the target of optimising the long-term pasture use. Moxnes *et al.* (1997) were able to demonstrate in their model that reindeer management focusing on optimal utilisation of reindeer pastures was also the most profitable in the long run. However, the stronger the unpredictable stochastic weather elements were, the lower the average economic returns from reindeer stock were.

Our study points to the fact that high reindeer densities on summer ranges reduced the body weights of reindeer calves and meat production per reindeer. Eventhough we did not get straight evidences that the economic carrying capacity of summer ranges have been exceeded in Finland it may be worth to worry about the limitation of summer fodder and summer pastures for the reindeer stock in question in some districts in the northern management area where carcass mass of slaughtering animals was lowest. This is becauce body mass and condition of animals in autumn are very important measures for reproduction of the stock and quality of slaughter animals.

High productivity of reindeer stock is achieved if the proportion of slaughtered reindeer in stock can be kept continuously high enough and the slaughtered animals are in good condition. This demands that there are a large proportion of highly productive females in good condition in the stock. If reindeer herding and management is based on natural pastures during the whole year, both the quantity and quality of winter and summer pastures and the long-term reindeer densities in these pastures affect decisively the productivity of reindeer stock. Therefore the fundamental question in reindeer management is finding the maximum long-term grazing pressure which is optimal to the quantity and quality of all reindeer pasture resources. Summer pastures may gradually develop into a limiting factor for reindeer stock productivity in some areas if overgrazed, and decreased winter pastures are only compensated for by supplementary feeding of reindeer.

Acknowledgements

We thank the Ministry of Agriculture and Forestry in Finland for supporting the pasture inventories, the data of which were also used in this study. We also thank the Association of Reindeer Herding Cooperatives for the reindeer husbandry statistics from the herding years 1993-99. We thank two anonymous referees and Øystein Holand of the Department of Animal Sciences in Agricultural University of Norway, Ås and Nicholas Williams of Sparsholt College, Hampshire, UK, for their valuable comments on the manuscript. We also thank Jukka Siitari from the Reindeer Research Station in Kaamanen for helping to handle the data. Finally we thank Carola Eklundh for checking the language of the manuscript.

References

Alpe, M. J., Kingery, J. L. & Mosley, J. C. 1999. Effects of summer sheep grazing on browse nutritive quality in autumn and winter. – *Journal of Wildlife Management* 63 (1): 346-354.

Augustine, D. J., Frelich, L. E. & Jordan, P. A. 1998. Evidence for two alternate stable states in an ungulate grazing system. – *Ecological Applications* 8 (4): 1260-1269.

Behnke, R. H. & Scoones, I. 1992. *Rethinking range ecology: implications for rangeland management in Africa. Overview of paper presentations and discussions at the Commonwealth Secreteriat tehnical meeting on savanna development and pasture production*, 19-21 November 1990, Woburn, UK. IIED, International Institute for Environment and Development, Paper No. 33, March 1992. 43 p.

Besley, D. A., Kuth, E. & Welsh, R. E. 1980. *Regression diagnostics: identifying influential data and sources of collinearity*. John Wisley & Sons, New York.

Caughley, G. 1976. Wildlife Management & the Dynamics of Ungulate Populations. – *In*: Coaker, T. H. (ed.). *Applied Biology* 1: 183-246.

Caughley, G. 1979. What is this thing called carrying capacity? – *In*: Boyce, M. S. and Harden-Wing, L. D. (eds.). *North American Elk: ecology, behaviour and management*. Cambridge University Press, Cambridge, pp. 159-187.

Caughley, G. & Lawton, J. H. 1981. Plant-herbivore systems. – *In*: May, R. M. (ed.). *Theoretical ecology*. Blackwell, Oxford, pp. 132-166.

Colman, J. E. 1999. New perspectives on reindeer rangeland management; equilibrium vs. non-equilibrium in an ecosystem dominated by dynamic interactions. – *Rangifer* Report No. 4: 58.

Colpaert, A. 1998. Satellite data and environmental GIS, from remotely sensed data to geographical information. Ph.D. thesis. – *Acta Universitatis Ouluensis* A 307.

Colpaert, A, Kumpula, J. & Nieminen, M. 1995. Remote sensing , a tool for reindeer range land management. – *Polar Record* 31 (177): 235-244.

Coulson, T., Albon, S. Guinness, F., Pemberton, J. & Clutton-Brock, T. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). – *Ecology* 78 (3): 852-863.

Crête, M. & Doucet, G. J. 1998. Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. – *Arctic and Alpine Research* 30 (2): 126-132.

Dasmann, R. F. 1981. *Wildlife biology*. Wiley, New York.

Ellis, J. E., Coughenour, M. B. & Swift, D. M. 1991. Climate variability, ecosystem stability, and the implications for range and livestock development. – *In*: Behnke, R. H., Scoones, I. & Kevern, C. (eds.). *Range ecology at disequilibrium: New models of natural variability and pastoral adaptation in Africa savannas*. ODI, London, pp. 31-41.

Fox, J. 1998. Finnmarksvidda: Reindeer carrying capacity and exploitation in a changing pastoral ecosystem – A range ecology perspective on the reindeer ecosystem in Finnmark. – *In*: *Commons in a cold climate, Series. Man and the biospere series*, Vol. 22, pp. 17-39.

Fynn, R. W. S. & O'Connor, T. G. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. – *Journal of Applied Ecology* 37: 491-507.

Hjeljord, O & Histøl, T. 1999. Range-body mass interactions of a northern ungulate - a test of hypothesis. – *Oecologia* 119: 326-339.

Helle, T. 1980. Laiduntilanteen muutos ja riskinotto Suomen poronhoidossa (in Finnish with English abstract: Changes in the state of grazing areas and risk taking in Finnish reindeer management). – *Lapin tutkimusseura Vuosikirja* XXI: 13-22.

Helle, T. & Kojola, I. 1994. Body mass variation in semidomesticated reindeer. – *Canadian Journal of Zoology* 72: 681-688.

Henry, G. H. R. & Gunn, A. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. – *Arctic* 44 (1): 38-42.

Hewison, A. J. M., Vincent, J. P., Bideau, E., Angibault, J. M. & Putman, R. J. 1996. Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. – *Journal of Zoology* London 239: 573-581.

Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. – *Journal of Wildlife Management* 32 (2): 350-367.

Klein D. R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. – *Journal of Range Management* 40 (4): 336-338.

Kojola, I., Helle, T., Niskanen, M. & Aikio, P. 1995. Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer *Rangifer t. tarandus* in Finland. – *Wildlife Biology* 1 (1): 33-38.

Kumpula, J. 1999. Developing an ecologically and economically more stable semi-domesticated reindeer management - a Finnish point of view. – *Rangifer* Report No. 3: 111-119.

Kumpula, J. & Nieminen, M. 1992. Pastures, calf production and carcass weights of reindeer calves in the Oraniemi co-operative, Finnish Lapland. – *Rangifer* 12: 93-104.

Kumpula, J., Colpaert, A., Kumpula, T. & Nieminen, M. 1997. Suomen poronhoitoalueen talvilaidunvarat (in Finnish with English abstract: The winter pasture resources of the Finnish reindeer management area). – *Kala- ja riistaraportteja*, nro 93, Riistan- ja kalantutkimus, Kaamanen, Finland. 42 pp., 11 app. and 34 maps.

Kumpula, J., Colpaert, A. & Nieminen, M. 1999. Suomen poronhoitoalueen kesälaidunvarat (in Finnish with English abstract: The summer pasture resources of the Finnish reindeer management area). – *Kala- ja riistaraportteja* nro 152, Riistan- ja kalantutkimus, Kaamanen, Finland, 40 pp. and 6 app.

Kumpula, J., Colpaert, A. & Nieminen, M. 1998. Reproduction and productivity of semidomesticated reindeer in northern Finland. – *Canadian Journal of Zoology* 76: 269-277.

Kumpula, J., Colpaert, A. & Nieminen, M. 2000. Condition, potential recovery rate and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. – *Arctic* 53 (2) 152-160.

Leader-Williams, N. & Ricketts, C. 1982. Growth and condition of three introduced reindeer herds on South Georgia: the effects of diet and density. – *Holoarctic Ecology* 5 (4): 381-388.

Leader-Williams, N., Smith, R. I. L. & Rothery, P. 1987. Influence of introduced reindeer on the vegetation of South Georgia: results from a long-term exclusion experiment. – *Journal of Applied Ecology* 24: 801-822.

Lehtonen, J. & Heikkinen, R. K. 1995. On the recovery of mountain birch after *Epirrita* damage in Finnish Lapland, with a particular emphasis on reindeer grazing. – *Ecoscience* 2 (4): 349-356.

Manseau, M., Huot, J. & Crête, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. – *Journal of Ecology* 84: 503-513.

Mattila, E. 1988. Suomen poronhoitoalueen talvilaitumet (in Finnish with English abstract: The winter ranges of the Finnish reindeer management area). –*Folia Forestalia* 713. 53 pp.

Mattila, E. 1996. Porojen talvilaitumet Suomen poronhoitoalueen etelä- ja keskiosissa 1990-luvun alussa (in Finnish). – *Folia Forestalia* 1996 (4): 337-357.

McCullough, D. R. 1979. *The George Reserve deer herd: population ecology of a K-selected species*. University of Michigan Press, Ann Arbor.

McCullough, D. R. 1992. Concepts of large herbivore population dynamics. – *In*: McCullough, D. R. & Barrett, R. H. (eds.). *Wildlife 2001: populations*. Elsevier, Essex, pp. 967-984.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? – *Oikos* 79 (3): 529-542.

Messier, F. 1995. Trophic interactions in two northern wolf-ungulate systems. – *Wildlife Research* 22: 131-146.

Messier, F., Huot, J., Le Henaff, D. & Luttich, S. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. – *Arctic* 41 (4): 279-287.

MMM, 1999. Porolukujen tarkistamistyöryhmän esitys suurimmiksi sallituiksi eloporoluvuiksi (in Finnish). – *Työryhmämuistio MMM* 1999: 20, Maa- ja metsätalousministeriö, Helsinki. 29 pp. and 72 app.

Moxnes, E., Danell, Ö., Gaare, E. & Kumpula, J. 1997. Reindeer husbandry: Natural variation and measurement error. – *SNF (Stiftelsen for samfunns- og næringslivsforskning) report* no. 59, Foundation for Research in Economics and Business Administration, Bergen, Norway. 42 pp.

Nieminen, M. & Autto, P. 1989. Porojen laitumet ja ruokinta poronhoitovuonna 1986-87. 2. Rehut ja ruokinta (in Finnish). – *Poromies* 56 (2): 38-43.

Ouellet, J.-P., Boutin S. & Heard, D. C. 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. – *Canadian Journal of Zoology* 72: 1426-1435.

Poromies, 1994-2000. Finnish journal *Poromies*, number 2 in each year with statistics of Finnish reindeer husbandry.

Post, E. & Klein, D. R. 1999. Caribou calf production and seasonal range quality during a population decline. – *Journal of Wildlife Management* 63 (1): 335-345.

Reimers, E. 1983. Growth rate and body size differences in *Rangifer*, a study of causes and effects. – *Rangifer* 3 (1): 3-15.

Sand, H., Bergström, R., Cederlund, G., Östergren, M. & Stålfelt, F. 1996. Density-dependent variation in reproduction and body mass in female moose *Alces alces*. – *Wildlife Biology* 2 (4): 233-245.

Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. – *Oecologia* 60: 156-168.

Skogland, T. 1985. The effect of density-dependent resource limitations on the demography of wild reindeer. – *Journal of Animal Ecology* 54: 359-374.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E. & Havas, P. 1992. Compensatory responses of a deciduous dwarf shrub, the bilberry (*Vaccinium myrtillus* L.) to simulated herbivory - some comparisons with the evergreen lingonberry (*Vaccinium vitis-idaea* L.). – *Acta Oecologica* 13:607-615.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E. & Havas, P. 1993. Above-ground growth response of the bilberry (*Vaccinium myrtillus* L.) to simulated herbivory. – *Flora* 188: 197-202.

Tolvanen, A., Laine, K., Pakonen, T., Saari, E. & Havas, P. 1994. Responses to harvesting intensity in a clonal dwarf shrub, the bilberry (*Vaccinium myrtillus* L.). – *Vegetatio* 110: 163-169.

Tyler, N. 1998. Reindeer pastures at disequilibrium. – *Rangifer*, Report No. 2: 67.

Wilkinson, L., Blank, G. & Gruber, C. 1996. *Desktop data analysis with Systat*. Prentice Hall, Upper Saddle River, New Jersey. 798 pp.

Wegener, C. & Odasz-Albrigtsen, A. M. 1998. Do Svalbard reindeer regulate standing crop in absence of predators? A test of the «exploitation ecosystems» model. – *Oecologia* 116: 202-206.

Manuscript received 28 April, 2000
accepted 9 November, 2001